SPACING BEHAVIOUR, TIME BUDGETS AND TERRITORIALITY IN RIFLEMAN (ACANTHISITTA CHLORIS CHLORIS) AND GREY WARBLER (GERYGONE IGATA) AT KOWHAI BUSH

A thesis submitted in partial fulfilment of

the requirements for the Degree

of

Master of Science

by

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University of Canterbury

1990

RIFLEMAN

GREY WARBLER

CONTENTS

ABSTRACT

Investigations of home range areas, time budgets and mate guarding behaviour were carried out, during two breeding seasons, on two species of small, insectivorous, native, New Zealand passerines. Rifleman *(Acanthisitta chloris chloris)* and Grey Warbler *(Gerygone igata)* differ in several aspects of their breeding biology from most small passerines, and this suggests that they are operating close to the energetic limits of small birds living in a moderate climate. The two species are very similar to each other with respect to size, diet and breeding biology but have different behavioural strategies with respect to territoriality and parental care. Grey Warblers are territorial and the male has no direct contribution to parental care until the nestling stage, at that time he helps the female to feed the chicks and later the fledglings. Conversely, Riflemen do not defend territories and the male makes a significant contribution to parental care through all the stages of the breeding season.

The effect that the different territorial and parental care strategies had on home ranges, time budgets and mate guarding behaviour in the two species was investigated. Riflemen were found to have exclusive home range areas that were maintained by mutual avoidance. Riflemen also had smaller home range areas during the pre-breeding and egglaying periods than later in the season, and this was interpreted as being a means of avoiding cuckoldry.

Grey Warbler males allocate a much smaller proportion of their time to feeding than female Grey Warblers or Riflemen, and the trade off for this was the time that they allocated to alert or guarding behaviour.

Grey Warbler males exhibited pronounced mate guarding behaviour, staying close to the female and below her. Male Riflemen spent more time at a distance to the female, but, like the male Grey Warblers, they tended to keep below the female.

The differences in the territorial behaviour and parental care of Riflemen and Grey Warblers are discussed in relation to differences in life history characteristics.

GENERAL INTRODUCTION

It has been hypothesised that animals should organise their behaviour to minimise total costs, in terms of genetic fitness, or to maximise total benefits (Krebs & Davies, p 315. 1978). If so their behaviour can be interpreted as sets of adaptations to the spatial and temporal patterning of the environment (Morse 1971). Certain sets of adaptations may be considered as adaptive strategies that can cut across community barriers and are in theory distinct from special adaptations to particular environmental regimes (Morse 1971).

The adaptive strategies that animals adopt to maximise their genetic fitness are largely dictated by ecological and morphological constraints. Different feeding strategies for example may be dictated by the range of variability of the food resource and the ability of an animal to exploit it (Morse 1971). Two different breeding strategies also show how the interaction of morphology and ecology can determine life history characteristics. Early repeated reproduction occurs in some of the estrildine finches and doves which first breed when they are a little less than 6 months old (Lack 1968). Delayed exhaustive breeding occurs in the Pacific sockeye salmon *(Oncorhynchus nerka)* which delays breeding until it makes an enormous self sacrificial breeding effort at about 3 - 7 years old. These different strategies are dictated by a combination of the stability of the environment, adult mortality rates and the potential for determinate growth of the adult (Horn 1978).

The social organisation of a species can also be viewed as an adaptation to prevailing environmental conditions. For example, two species of corvids in the southwestern United States exhibit very different social systems which may be viewed as different solutions to the problem of spatio-temporal variability in food resources (Marzluff & Balda 1988). Scrub jay *(Aphelocoma coerulescens)* pairs defend classic, year round all purpose territories, whereas pinyon jays *(Gymnorhinus cyanocephalus)*

live in integrated, social flocks throughout the year, nest in colonies, occasionally have helpers at the nest, and only defend an area immediately around the nest (Marzluff & Balda 1988). Scrub jays are generalist feeders that use whatever resources are available within their home ranges. Small home ranges that supply a variety of foods are economically defendable thereby providing suitable conditions for territoriality to evolve. Pinyon jays are specialised feeders that eat pinyon pine *(Pinus edulis)* seeds and fly long distances in search of places with abundant seeds. Locally abundant but widely scattered crops are not economically defendable, and pinyon jays did not become territorial.

In this study, I investigated two species of bird that operate under similar ecological and morphological constraints, have many similarities in size, diet, and breeding biology, but apparently have different strategies with respect to parental care and territoriality. Rifleman *(Acanthisitta chloris chloris)* and Grey Warbler *(Gerygone igata)* are New Zealand's smallest birds. Both weigh between 5 and 7 gms, with individual seasonal variation of up to 1 g (Gill 1980; unpub. Kowhai Bush nest records). Both species are insectivorous, and at Kowhai Bush feed mostly on species of adult lepidoptera, diptera, and arachnida which together form about 94% and 81% of their diet. For Grey Warbler the remaining 6% is comprised of coleopterans, hemipterans, and lepidoptera larvae, whereas for the Rifleman the remaining 19% is comprised of coleopterans, neuropterans, hemipterans, orthopterans, molluscans, amphipods, isopods, myriapods, hymenopterans, and lepidoptera larvae (de Hamel 1989).

Both species have relatively high fecundity. The mean clutch size of 4.4 represents about 85% of the female Riflemans body weight (Sherley 1985), whereas the mean Grey Warbler clutch size of 3.9 (Gill 1980) is about 91% of female body weight (Sherley 1985). The laying interval for each of the two species of 48 hours is in contrast to the 24 hour laying interval of most small passerines (Lack 1968).

Comparable data for the ratio of clutch size to percent female body weight in three other small, native, insectivorous passerines at Kowhai Bush are: New Zealand Robin *(Petroica australis)* 2.7:35%, Brown Creeper *(Finschia novaeseelandiae)* 3.7:67% and Fantail *(Rhipidura fuliginosa)* 3.5:66%. All three of these species also have a 24 hour laying interval (Sherley 1985).

Rifleman and Grey Warbler are both sedentary birds and individual home ranges do not usually change significantly, either seasonally or between years (Gill 1980, unpublished Kowhai Bush nest records). Long term pair bonds occur in both species, with the same individuals remaining together for several years, in many cases until one or other partner dies (Gill 1980, unpublished Kowhai Bush nest records). Lack (1968) suggested that mating for life was rare among passerines, however, annual mortality rates in New Zealand birds are much lower than in the northern hemisphere, perhaps explaining why long term pair bonds are documented more readily in New Zealand. Gill (1980) estimated that annual mortality of Grey Warblers at Kowhai Bush was about 18.5%, and an estimate of about 40% for Rifleman in the same bush was made by Sherley (1985). Grey Warblers defend both their territories and mates. The male Grey Warbler sings, and is frequently observed in aggressive intra-specific interactions such as chasing and fighting. Conversely, Rifleman do not sing, for reasons that are unclear. Although the Rifleman syrinx lacks intrinsic muscles (Sibley et al. 1982), this does not necessarily mean a physical inability to sing since the Lyrebird *(Menura sp.)* has a similar syrinx (Feduccia & Olson 1982) and a remarkable song (Slater 1974). Also Rifleman are rarely seen interacting aggressively. Sherley (1985) noted that both male and female Rifleman spend less than 1% of their time during the prelaying and egglaying periods involved in "territorial disputes". In contrast he found that males of New Zealand Robin *(Petroica australis)* spent about 17% of their time vocalising and defending territories during the prelay period, and 6% during egglaying. Female Robins on the other hand spent much less time on these activities.

Rifleman are often seen very close to their neighbours during the breeding season and their apparently indifferent behaviour at such times suggests they are not territorial (Sherley 1985; pers.obs).

Another way in which Rifleman and Grey Warbler differ is in the amount of parental care provided by males. The male Rifleman helps build the nest, he courtship feeds the female (meeting the extra nutritional and energetic demands for egg laying), shares incubation and brooding with the female, and feeds nestlings and fledglings (Sherley 1985). However, the male Grey Warbler has no direct input into parental care until the nestling stage, when he helps to feed the nestlings and later the fledglings (Gill 1980). This type of pattern in which the female builds the nest, incubates the eggs and broods the nestlings, but both parents share the feeding and defending of the young is common in territorial passerines (Wolf et al. 1988).

I have investigated how the different strategies of parental care and territoriality adopted by Riflemen and Grey Warblers affected the home ranges, time budgets and mate guarding behaviour of the two species, and discuss the differences in their life histories which could have lead to the different strategies.

In section 4 I examine how the different activity demands of territorial behaviour and parental care affected the time budgets of the two species, and how they varied between the sexes.

In section 5 I compare the relative sizes of the home ranges of Rifleman and Grey Warbler, and the extent of overlap between neighbouring pairs.

In section 6 I compare the mate guarding behaviour of the two species during the pre-breed and egglaying periods.

The discussion for all the data sections is contained in section 7.

TAXONOMY

DNA-DNA hybridisation studies suggest that Rifleman and Grey Warbler belong to separate suborders of the order Passeriformes, the Tyranni (suboscines) and the Passeri (oscines) respectively (Sibley et al.1988). However, Raikow (1987), placed them both in the suborder Passeres (oscines) on the basis of hind limb musculature. Although disagreeing on whether the New Zealand wrens, which include Rifleman, are a sister group of the oscines or the suboscines, both methods suggest that the acanthisittids are the descendants of an ancient lineage whose origin is separate from that of the other suboscine groups (Raikow 1987). The branching which gave rise to the groups to which Rifleman and Grey Warbler belong occurred very early in passerine radiation, at least 50 million years ago (Sibley & Ahlquist 1985).

In the family Acanthisittidae, to which the Rifleman belongs, four genera containing six species have been described. All are or were endemic to New Zealand. However, *Pachyplichas jagmi, P. yaldwini* and *Traversia lyalli* are now extinct, *Xenicus longipes* is probably extinct, and *X. gilviventris* is rare (Millener 1988). Only the Rifleman *(Acanthisitta chloris)* has maintained a wide distribution and high population numbers despite habitat modification and the presence of introduced predators (Gray & Gaze 1985). The Rifleman is the smallest and most able flyer of the group (Millener 1989), and its ability to fly may have contributed to its continued survival. Two subspecies of Rifleman are recognised, the North Island Rifleman *(A.chloris granti)* and the South Island Rifleman *(A.chloris chloris)*, in addition to having non-overlapping geographical distributions they differ slightly from each other in colouration and voice (Gray & Gaze 1985).

The Grey Warbler belongs to the tribe Acanthizini, of the subfamily Acanthizinae family Pardalotidae. The tribe contains four genera, including *Gerygone* (Sibley et al. 1985, 1988) which has seventeen described species in Australia, New

Guinea and New Zealand (MacDonald 1973; Ford 1981). The Grey Warbler *(G. igata)* and the Chatham Island Warbler *(G. albofrontata)* are the only species found in New Zealand, and both are endemic to this country.

STUDY AREA AND GENERAL METHODS

Study area

Kowhai Bush is situated on the east coast of South Island New Zealand about eight kilometers north-west of the township of Kaikoura (N.Z.M.S.260, 031 605705). It is a narrow strip of kanuka/broadleaf forest covering 240 ha of flat, river gravels on the north-eastern side of the Kowhai River (Hunt & Gill 1979).

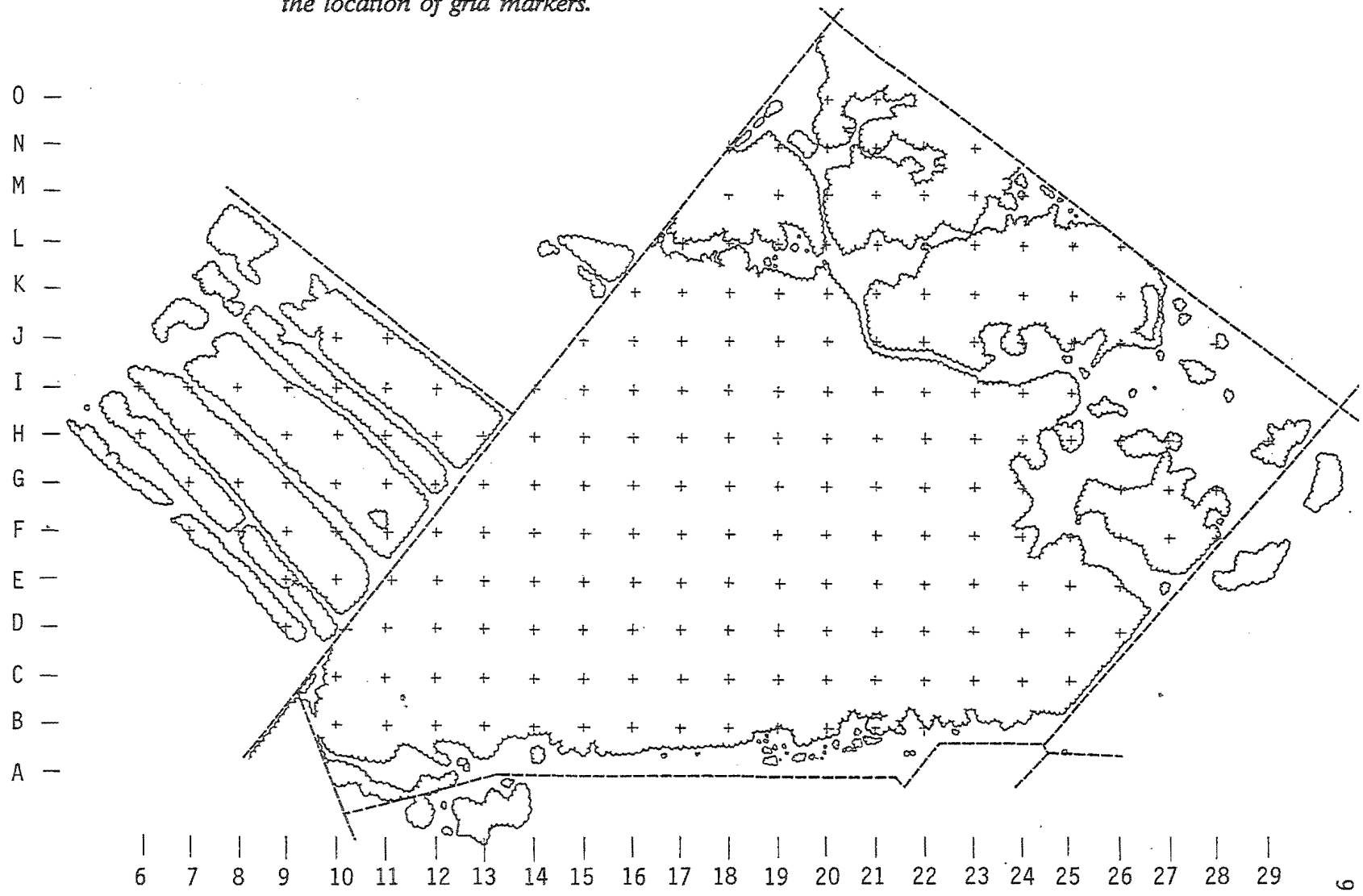
The climate of the area is characterised by moderate winters and warm summers, with an average temperature of 7.4 C in the coldest month, July, and 16.1 C in the warmest month, February. However, the district also experiences seasonal extremes. During the winter, southerly changes can bring sudden showers of rain, hail, sleet and occasionally snow. Low rainfall and drought conditions in summer are accentuated by strong northwesterly winds that are hot and dry and can produce day temperatures above 32 C (Gill 1980, Sherley 1985).

My study was confined to an area of 20.25 ha extending into farmland adjacent to the Kowhai Bush reserve. The dominant vegetation type was kanuka *(Kunzia ericoides)* growing to an average height of 5-7 m. The area was grazed by sheep and cattle, and consequently there was very little understorey vegetation. Occasional tutu *(Coriaria arborea)* and gorse *(Ulex europeaus) bushes* occured, but otherwise the forest was open, allowing quick easy movement and good visibility, conditions that greatly facilitated the following of birds.

A 30 m grid had already been marked out in the study site, and the numbered and lettered axes enabled each grid square to be identified (Fig.1).

About 66 nest boxes were distributed at grid locations within the study site. With one exception in the second season, all Rifleman in the study area used these nest boxes for breeding.

Figure. 1 *Study site at Kowhai Bush showing the location of grid markers.*



General Methods

Birds were banded with N.Z.D.O.C. numbered aluminium leg bands and coloured plastic leg bands in unique combinations. During the study, 35 Riflemen had leg bands and each year only three were unbanded. Of the banded individuals, 17 were present in both years, and one of the unbanded ones seen each year was probably the same individual because it was with the same partner in the same area each year. Six pairs stayed together over both seasons, and of the remaining 9 pairs from the first season one or both members had disappeared. Twenty male Grey Warblers had leg bands and only one was unbanded. Of the banded male Grey Warblers, 12 were present in both seasons, and one unbanded individual (probably the same bird) in the same territory each year. He was wary of the mist net and could not be caught. Of 18 and 19 female Grey Warblers present each year, only four were banded. Three of them were present in both seasons, and the fourth was banded in the second season. Of the 3 Grey Warbler pairs in which both the male and female were banded in the first year, the same individuals formed pairs in the second year.

Many of the birds had been banded in previous years and some birds were known to be up to five years old. One Rifleman, banded as an adult in 1981, was at least nine years old.

To capture Grey Warblers, two 9 m long mist nets were hung one on top of the other between two poles, so they were distributed from near the top of the canopy to just above the ground. Recordings of calls or songs were played back through speakers on each side of the net. They could be switched on or off independantly and remotely depending on the side from which the bird approached. Male Grey Warblers responded well to playback but females did not, explaining why only four female Grey Warblers were banded. Some Riflemen were caught by placing a net across the entrance to the nestbox when they were feeding chicks, however, most were banded on the nest as chicks. No Rifleman nests were abandoned after birds were captured

near the entrance. Some female Grey Warblers were also caught by placing nets near nests, however, the success of this method was dependent on having chicks in the nest, and few Grey Warblers got to the nestling stage. Therefore few adult female Grey Warblers were banded with this method either. All chicks were banded before they fledged. Every time birds were handled their weights were recorded, and bill, wing and tarsus measurements of adults were also made.

Most Grey Warbler nests were found while the female was building. Nest building behaviour, especially early in the season when first nests were being built, was obvious and birds were easy to follow. A pair, easily located by the male song, fed together for a while and then the female would suddenly gather nest material and move rapidly towards the nest. An observer could then find the nest easily if the bird was not lost to sight. Several attempts to follow the bird were often necessary, because it was easy to lose sight of a flying bird. When a nest was found, a nearby tree was tagged and information was recorded about the nests grid location, its height, the height of the tree it was in, the height of the surrounding canopy, and the percentage of cover it got from the surrounding foliage. These were all visual estimations.

Nests were checked every few days to determine the stage of breeding. This was straightforward for Rifleman as the nest boxes were at about head height and the nest could be inspected using an ophthalmoscope to peer through the nest entrance. Grey Warbler nests were usually 2 - 7 meters up in Kanuka trees however, and access to them was by a free standing ladder supported by ropes. Grey Warbler nests were pendulous and enclosed, and their contents were felt carefully with a finger, or inspected with the ophthalmoscope.

TIME BUDGET

INTRODUCTION.

In many animals food can limit reproductive success and survival, both in summer and winter (Martin 1987). Consequently, a large proportion of an animal's time may be taken up with foraging, and there may be little time available for other activities.

Failure to allocate time effectively to conflicting objectives may lead to decreased survivorship. For example, inattention to vigilance could result in not observing a predator and consequent death by predation (Bertram 1978). On the other hand, too much attention to vigilance or any other conflicting demand may result in reduced foraging time and starvation (Sullivan 1988, 1990). The relationship between efficient time budgeting and survival suggests that time budgeting might have a strong selective influence.

Wilson (1975) suggested that time-energy budgets evolve to fit periods of food shortage, and that the major requirements of animals differ greatly in the amounts of time and energy that it is profitable to devote to them in terms of maximising genetic fitness. Schoener (1971) suggested two contrasting strategies for food limited species which result in very different time-energy budgets and social organisation; time minimisation, for which a predictable reliable amount of energy is available so long as the energy source is protected, and energy maximisation, where all available energy is consumed regardless of the cost in time. Time minimisers minimise the amount of time required to harvest available energy, and the remaining time can therefore be devoted to other activities, including defending the food supply from intruders. Animals with a relatively fixed reproductive output per season (constant clutch size and brood number for example) are time minimisers, as are some species of insects, fish and birds that maintain feeding territories. Energy maximisers are usually

opportunistic species which grow and breed rapidly whenever they encounter suitable conditions. They tend to disperse widely and move from one temporarily suitable patch of the environment to another. Examples of energy maximisers can be found in the inland areas of continents, such as Australia and Africa (Dr. J. Wareham pers.comm). Many animals that have been dormant or have not bred for long periods in the dry areas of Australia will become active and start breeding after a period of rain. The banded stilt *(Cladorhyncus leucocephalus)* for example, which nests collonially on sand banks in the Southern half of Australia, when inland salt lakes are in flood (Slater 1970).

Strategies for balancing energy expenditure and intake vary greatly according to the size and metabolic requirements of the animal (Schoener 1971). Small homeotherms must balance their energy budgets over relatively short periods of time (Wolf et al., 1975), whereas large homeotherms can store energy endogenously (Wilson 1975). The metabolic requirements of poikilotherms are lower than those of homeotherms; for example, fish may need to eat only 2-4 % of their body weight in food per day, whereas shrews must consume close to their entire body weight (Schoener 1971).

The time strategy that an animal has adopted must reflect the ecological and morphological constraints under which the animal operates. Analysis of the ecology, morphology, and life history of an animal provides an evolutionary explanation for the details of its time budget (Wilson 1975). In colonies of social insects, for example, the requirement for a constant temperature in the nest and the need to repel invaders accounts for the seemingly aimless patrolling through the nest of many workers. They are assessing the needs of the colony from moment to moment and are thus able to respond to local requirements with little delay (Lindauer 1961, Michener 1964, cited in Wilson 1975). Elephant seals on their haul out grounds during the mating season are another example of how the effects of ecology and morphology can determine life

history characteristics, or adaptive strategies. Elephant seals have no serious food problems, because they have ample fat reserves, and have little or no problem with predators, consequently they concentrate almost entirely on reproduction while on their haul out grounds (Wilson 1975).

Conversely, one might expect analysis of time budgets to reflect something of an animals' life history. Therefore in this study, I investigated the time budget of the Rifleman and Grey Warbler to see whether they reflected aspects of territoriality in the two species. I predicted that:

i) The more territorial species, Grey Warbler, would spend more time guarding it's territory and defending its mate than the apparently non-territorial Rifleman.

ii) The time saved by male Rifleman through not defending a territory would be taken up with extended parental care.

I also asked:

i) How was allocation of time differentiated between the sexes and the species?

ii) How did different activity demands during the breeding season affect time budgets?

METHODS

Time budget data were obtained using instantaneous sampling techniques on focal animals. During a 10 minute sampling period instantaneous samples of behaviour were recorded every minute on to a tape recorder. Tapes were transcribed daily.

Data were recorded on birds when they were away from the nest, that is, not incubating or brooding.

Ten behaviour categories were recorded in the field. These categories were later combined into seven categories to allow more direct comparison between the sexes and the species.

The final seven behaviour categories were as follows:

1. Foraging/Feeding.

2. Nest building or nest maintenance. Building and maintenance were not differentiated. For Rifleman some of the activity in this category, later in the season, involved building second nests and some involved maintenance. Grey Warbler did not maintain nests after they were built.
3. Flight. Defined as when birds flew more than five meters. Less than five meters and it was still considered to be either foraging or alert perching.
4. Nothing. Where birds perched and were inactive.
5. Preening.
6. Alert perching. Where birds were perching and looking from side to side, successively changing their orientation or hopping from perch to perch in a manner indicating alertness vigilance or guarding. Alert perching was quite distinguishable from foraging hops or perching doing nothing. Singing was also included in alert perching.
7. Feeding nestlings. (Fledging data were not included in the analysis because too few data from the fledging period were available).

Courtship feeding by Riflemen was included with foraging and feeding because, regardless of which bird eats the item, courtship feeding still entails foraging and feeding. Guarding and singing by male Grey Warblers were included in the alert perch category because guarding and behaviour concurrent with singing were very similar to alert perching.

Two thousand and thirty one behavioural records were entered in a data base for 47 individual birds, with an average of 43 scans (1 minute samples) per bird. The percentage of time each behaviour was encountered for each individual was

calculated. and the Mann Whitney U test was used to test for significant difference in percent allocation of each behaviour between sexes and species.

Because significant differences in feeding allocation occurred between Riflemen and Grey Warblers the average non feeding time was not comparable. Therefore feeding data were removed and percentages were recalculated so I could analyse time allocated to non feeding behaviours alone.

Division of the non feeding data set into breeding stages resulted in sample sizes too small for statistical analysis, therefore comparison was restricted to early and late nesting: early nesting included pre-breed and egg laying periods, late nesting included incubation and nestling periods.

Individuals for which there were fewer than seven behavioural observations per period were excluded from the analysis (this occurred when the data set was subdivided either by removal of the feeding data, or into early and late nesting periods).

Because of the very large proportion of time spent on feeding the non-feeding behaviours were uncommon, and there were a large number of zero values amongst these data. The large number of zero values meant that variances were high and consequently statistical significance was not found for many of the differences in behaviour allocation. However, the overall patterns have been discussed whether statistically significant or not.

The birds were sampled when they were moving slowly through the bush and the comparisons were only of this type of activity. Riflemen and female Grey Warblers also allocated time to incubation and brooding, which was not included in the sampling. Male Grey Warblers allocated time to patrolling the territory, and at such times were impossible to follow, consequently patrolling behaviour was not included in the sampling. Patrolling behaviour was characterised by a series of long flights interspersed with short stops during which the bird would look around in the manner

of alert perching, and usually sing.

RESULTS

Interspecific Comparison

Male Riflemen, female Riflemen and female Grey Warblers allocated the majority of their time to feeding, whereas male Grey Warblers spent less than half of their time feeding (Fig.1). The male Grey Warblers allocated a larger proportion of time to alert perching and a smaller proportion to preening than the others did. Female Grey Warblers allocated a smaller proportion of time to flying and a larger proportion to preening and alert perching than did the Riflemen (Fig.2). Male Riflemen, on average, allocated a larger proportion of time to nest building and maintenance than either of the females. Table 1 gives the statistical significance of the differences. (See apendix 1 for means and standard errors).

Table 1. *Results of Mann Whitney U tests comparing the proportion of time spent on different behaviours. Comparisons were between female Riflemen and female Grey Warblers, and male Riflemen and male Grey Warblers.*

	Females		Males	
Behaviours	U	P	U	P
Foraging	0.72	N.S.	4.06	***
Nestbuilding	0.04	N.S.	1.85	N.S.
Flight	2.23	*	1.05	N.S.
Nothing	0.45	N.S.	1.63	N.S.
Preening	0.04	N.S.	0.65	N.S.
Alert Perching	0.23	N.S.	4.06	***
Feeding Chicks	1.32	N.S.	0.55	N.S.

N.S. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

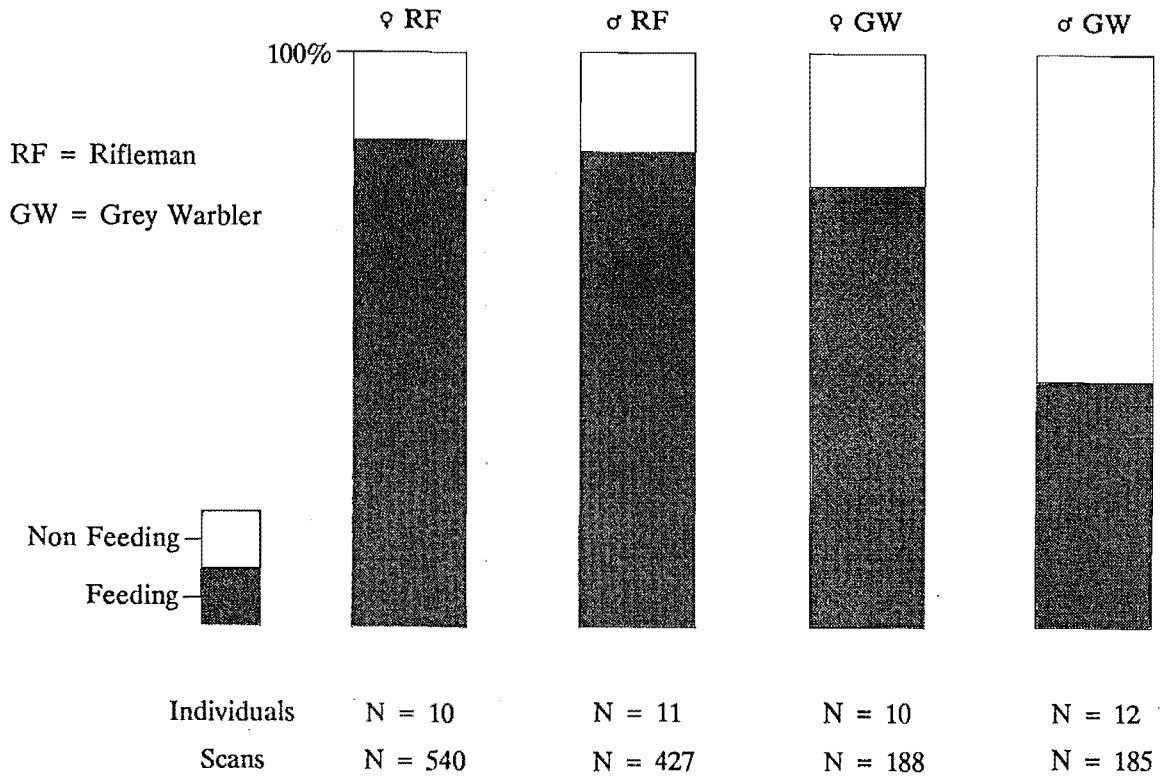


Figure 1. *The average percent of time allocated by riflemen and grey warblers to feeding.*

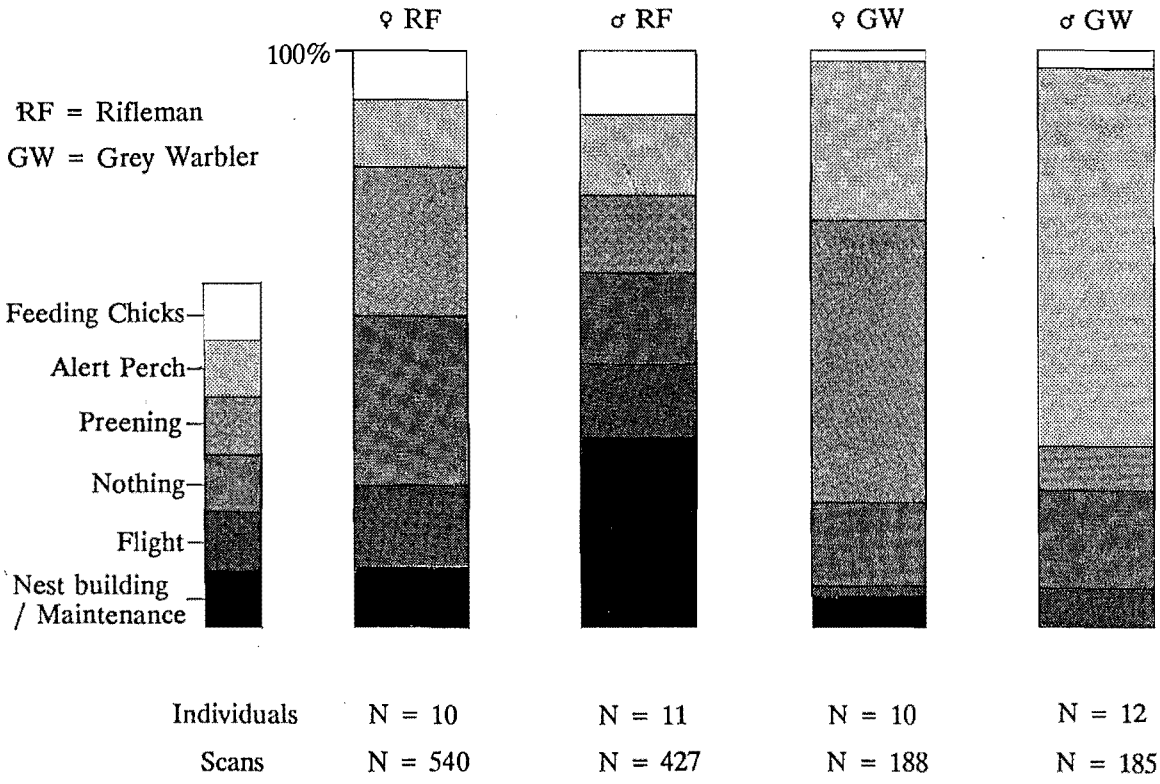


Figure 2. *The average percent of time allocated by riflemen and grey warblers to non feeding behaviours.*

Intraspecific Comparison

Female and male Riflemen both spent the majority of their time feeding, in both the early and late parts of the nesting period (Fig.3). Male Riflemen allocated a larger proportion of time, on average, to nest building than females, in both the early and late parts of the nesting period. Females allocated a larger proportion of time to preening in the early period, and nothing in the later period, than males (Fig.4). Table 2 gives the statistical significance of the differences.

Female Riflemen allocated a larger proportion of time to nest building, nothing and alert perching in the early period than in the late period. Male Riflemen allocated larger proportions of time to nest building and nothing, and smaller proportions to alert perching in the early period, than they did in the late period. (Fig. 4). Table 3 gives the statistical significance for these values. (See apendix 2 for means and standard errors).

Table 2. *Results of Mann Whitney U tests comparing the proportions of time spent on different behaviours between male and female Riflemen. (See methods for definition of periods).*

	Whole period		Early Period		Late Period	
Behaviour	U	P	U	P	U	P
Foraging	0.42	N.S	0.31	N.S.	0.38	N.S.
Nestbuilding	0.57	N.S.	1.28	N.S.	0.26	N.S.
Flight	0.14	N.S.	0.57	N.S.	0.19	N.S.
Nothing	0.49	N.S.	0.40	N.S.	1.34	N.S.
Preening	0.70	N.S.	1.10	N.S.	0.19	N.S.
Alert Perch	0.84	N.S.	0.22	N.S.	1.66	N.S.
Feeding Chicks	0.07	N.S.	----	-----	0.19	N.S.

*N.S. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.*

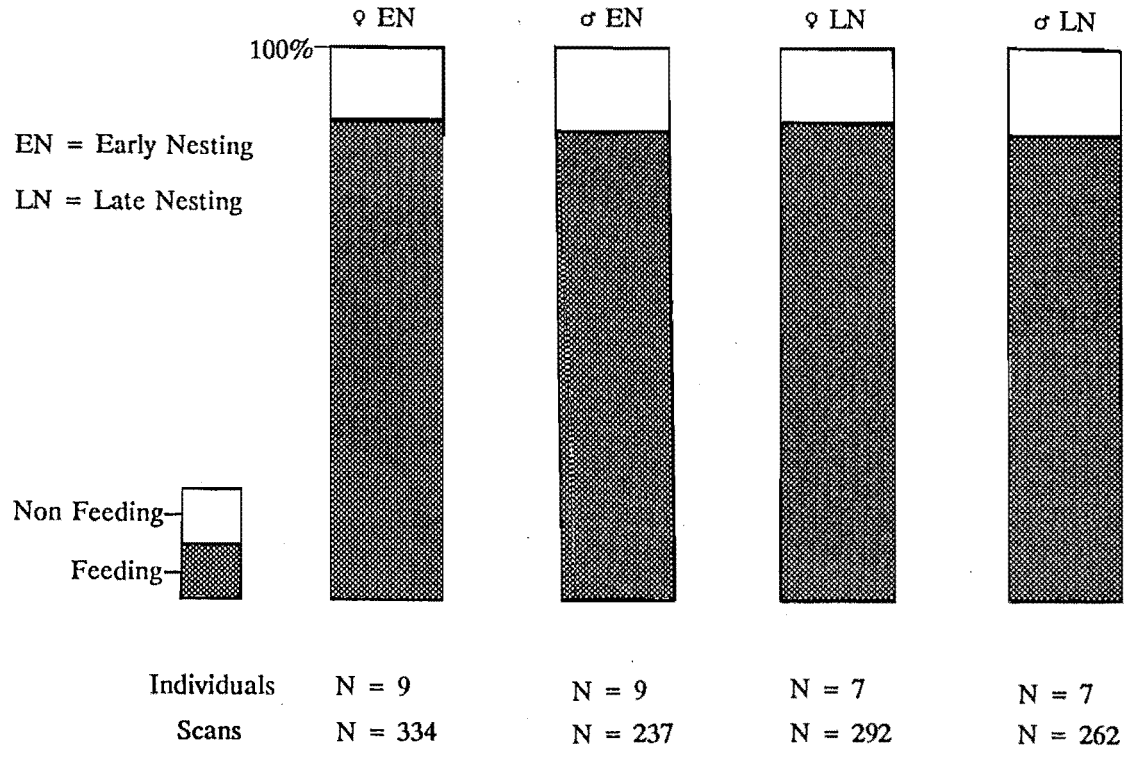


Figure 3. *The average percent of time allocated by riflemen to feeding behaviours, in the early and late parts of the nesting period.*

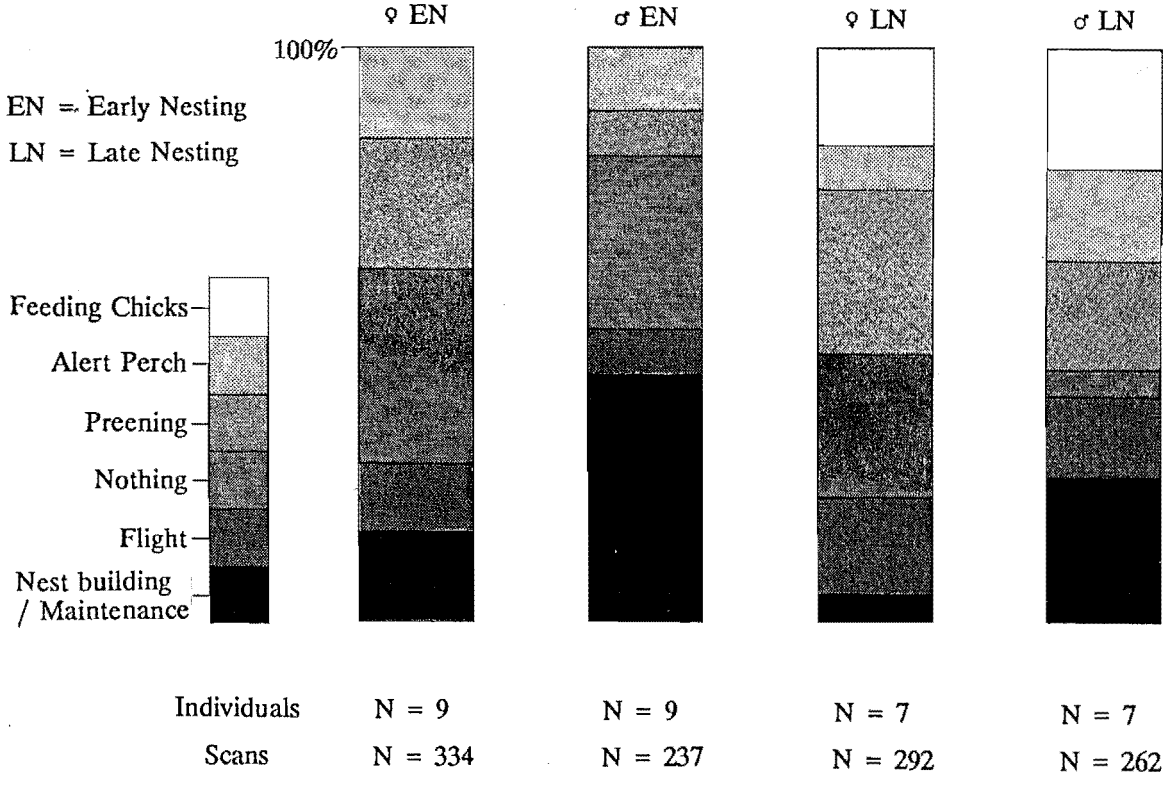


Figure 4. *The average percent of time allocated by riflemen to non feeding behaviours, in the early and late parts of the nesting period.*

Table 3. *Results of Mann Whitney U tests comparing the proportion of time spent on different behaviours between the early and late parts of the nesting period. Female Riflemen were compared between early and late periods, and male Rifleman between early and late periods.*

	Female		Male	
Behaviour	U	P	U	P
Foraging	0.16	N.S	0.16	N.S.
Nestbuilding	0.00	N.S.	0.90	N.S.
Flight	1.64	N.S.	0.69	N.S.
Nothing	0.37	N.S.	1.80	N.S.
Preening	0.58	N.S.	1.43	N.S.
Alert Perching	0.63	N.S.	1.11	N.S.
Feeding Chicks	----	-----	----	-----

N.S. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Female Grey Warblers allocated the largest portion of their time to foraging in both the early and late parts of the nesting period, and their allocation was more than that of the male in both periods (Fig. 5). Male grey Warblers do not help to build the nest so the males had more discretionary time to devote to other behaviours. The males allocated a larger proportion of time to alert perching and flying than the females did, in the early part of the nesting period, and the females allocated a larger proportion of time to preening (Fig. 6). Table 4 gives the statistical significance for these differences.

The sample size for female Grey Warblers during the late part of the season was too small to allow reliable inference about how female Grey Warblers allocated their time during that period. However, male Grey Warbler feeding allocation decreased slightly during the late nesting period, whereas the female allocation, remained similar to that during the early nesting period (Fig.5). It is probable that the

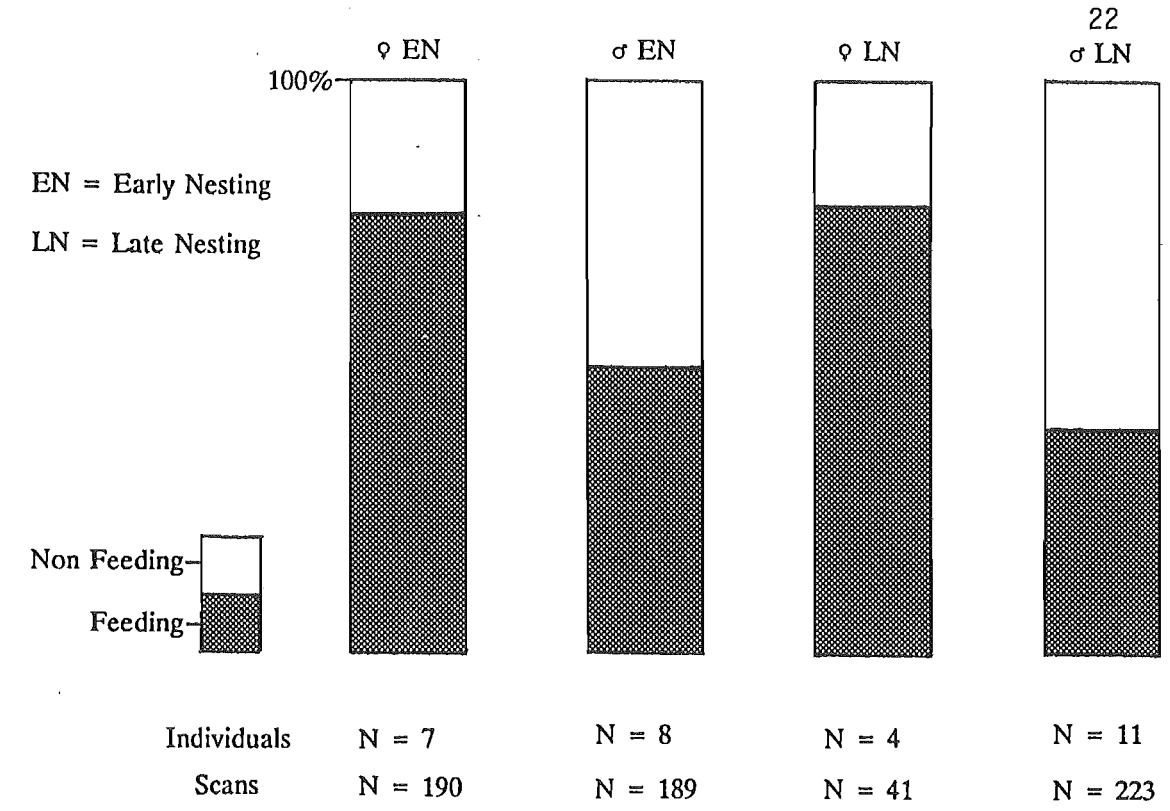


Figure 5. *The average percent of time allocated by grey warblers to feeding behaviours, in the early and late parts of the nesting period.*

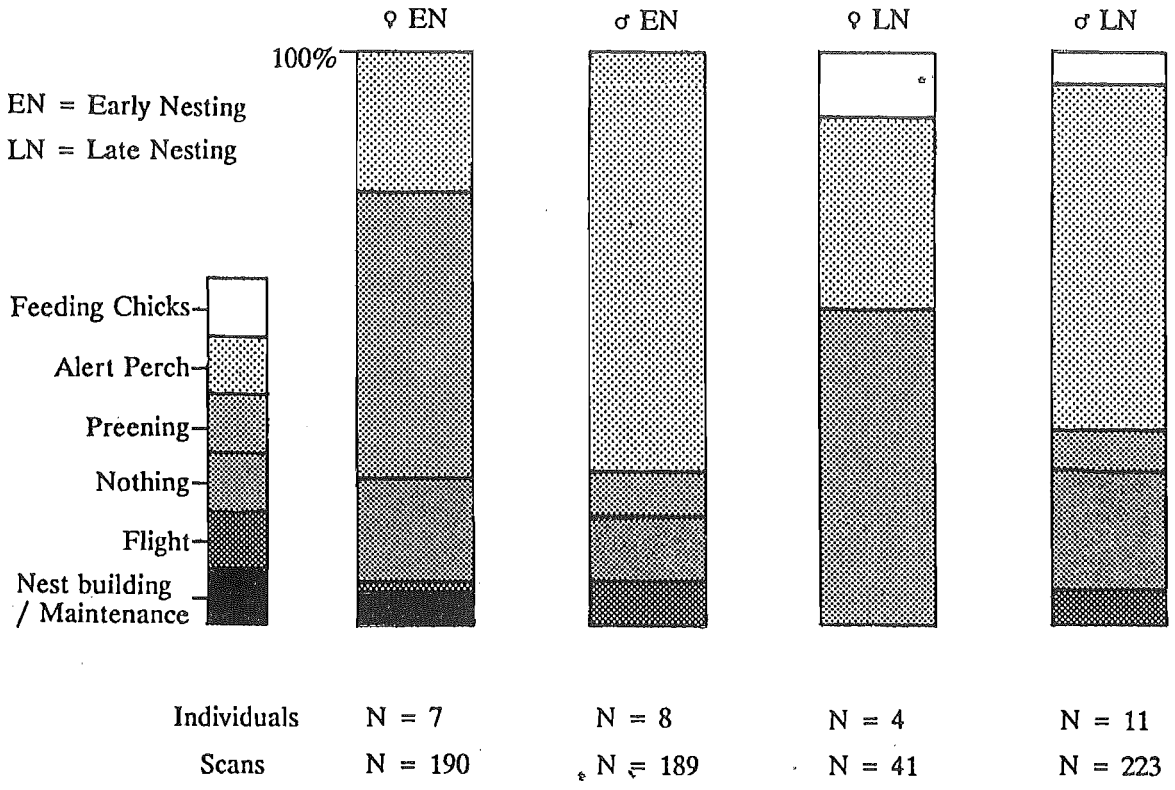


Figure 6. *The average percent of time allocated by grey warblers to non feeding behaviours, in the early and late parts of the nesting period.*

female also fed more in the late nesting period.

Male Grey Warblers allocated a larger proportion of time to feeding, and a smaller proportion to doing nothing in the earlier part of the nesting period than in the later (Fig. 6). Table 5 gives the stastical significance of these differences. (See appendix 3 for means and standard errors.).

Table 4. *Results of Mann Whitney U tests comparing the proportion of time spent on different behaviours between male and female Grey Warblers. (See methods for definitions of periods).*

	whole period		early period	
Behaviour	U	P	U	P
Foraging	3.82	***	2.60	**
Nestbuilding	1.19	N.S.	0.93	N.S.
Flight	2.37	*	1.39	N.S.
Nothing	1.32	N.S.	0.81	N.S.
Preening	1.16	N.S.	0.12	N.S.
Alert Perch	3.96	***	3.01	**
Feeding Chicks	0.56	N.S.	----	-----

N.S. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Table 5. *Results of Mann Whitney U tests comparing the proportion of time spent on different behaviours, for male Grey Warblers, between the early and late parts of the nesting period.*

	Male Grey Warbler	
Behaviour	U	P
Foraging	1.73	N.S.
Nestbuilding	0.00	N.S.
Flight	0.37	N.S.
Nothing	1.53	N.S.
Preening	0.16	N.S.
Alert Perching	0.58	N.S.
Feeding Chicks	----	-----

N.S. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

SUMMARY OF RESULTS

Male Grey Warblers fed much less than Riflemen or female Grey Warblers and this appears to be mostly traded off against alert perching. The reasons for this may lie with the activities outside those which were sampled (refer to methods for explanation). The Riflemen and the Female Grey Warbler spent the 'extra-to-sample' time incubating or brooding, which not only used energy (Sherley 1985), but also took time out from harvesting energy, or feeding. The male Grey Warbler, on the other hand spent 'extra-to-sample' time patrolling which although using energy, would still allow for opportunistic feeding.

Male Grey Warblers, spent more time alert perching than male Riflemen or female Grey Warblers, and they also spent time patrolling their territory. Riflemen and female Grey Warblers did not patrol. However, female Grey Warblers did allocate a larger proportion of their time to alert perching. There is probably a component of alert perching which has no connection with guarding or vigilant behaviour, but may be a response to a noise, a moment of decision making or observation of the observer. A large proportion of riflemens alert perch allocation might be represented by these unknowns, however at least the amount of the difference between Riflemen and female Grey Warblers is probably attributable to vigilance. Female Grey Warblers may be looking out for predators rather than guarding the territory, except close to the nest which they may defend.

The larger preening component of the female Grey Warblers time budget may imply that they have more discretionary time than Riflemen or male Grey Warblers. This would be especially so during the nestling stage because female Gray Warblers allocated a smaller proportion of time to feeding chicks. A lower chick feeding allocation for female Grey Warblers was probably partly because they had fewer chicks to feed, but also because they have a lower feeding rate of chicks than Riflemen, de Hamel (1989) found that Riflemen fed chicks at a rate of 197.9

feeds/chick/day (f/c/d), whereas the rate for Grey Warblers was 75.0 f/c/d when feeding Grey Warbler chicks and 220.1 f/c/d when feeding Shining Cuckoo *(Chrysoccyx lucidus)* chicks (Grey Warbler are parasitised by Shining Cuckoos). None of the Grey Warbler nests that time budget data were collected for was feeding a cuckoo.

Male Riflemen do most of the building of the second nest. Grey Warblers did not maintain their nests after they had been built, whereas Rifleman would bring additional material to the nest all through the season and would take feathers in and out to dry them. Higher rates of nest building and nest maintenance by Rifleman are probably a consequence of enclosed nests that don't breath and are therefore subject to condensation.

HOME RANGE

INTRODUCTION

The dispersion of animals in space and time is a consequence of the response of individuals to features of the environment and to the presence or absence of other members of the species. The degree to which home ranges overlap intraspecifically varies among different species, in some there is no overlap, while in others overlap is nearly complete. Non overlap is usually a consequence of territorial behaviour, such as defense or advertisement, but can also be caused by mutual avoidance or preference for an unexploited food supply (Brown & Orians 1970, Davies 1978). Some writers also consider the latter two behaviours to be evidence of territoriality (Shoener 1968, Pitelka 1959 cited by Brown & Orians 1970 & Schoener 1968). Population density and the relative intensity of competition for space have some effect on spacing behaviour (Brown & Orians 1970).

Whether an animal defends its home range or not is dependent on the balancing of costs and benefits (Davies 1980, Wilson 1975, Hinde 1956, McLean & Seastedt 1979). Brown (1964) (cited in Brown & Orians 1971), suggested that territorial defence is likely to occur if the geographic distribution of the resource allows the animal to defend it and receive some net benefit in terms of fitness. Energy expended in territoriality is often high compared to other activities and depletion of energy reserves over the mating season may constrain behaviour and reproductive success (Marden & Waage 1990). Energetic costs are known to influence the way animals defend territories (Davies & Houston 1984). Costs of territorial defence include the energy expended on fighting or displaying and time lost to direct enhancement of reproduction (Marden & Waage 1990, McLean & Seastedt 1979). Some benefits of territorial defence are the exclusive use of a food resource, increased likelihood of

attracting a mate and reduced interference with mating.

In this study I mapped the home ranges of Riflemen and Grey Warblers during the breeding season. The Grey Warbler is territorial, the male advertises it s territory by singing, and actively chases out intruders. The Rifleman appears not to be territorial, it does not sing, is rarely seen in aggressive interaction and appears to tolerate the close proximity of neighbours during the breeding season. I compared the relative sizes of the home ranges of the two species and the amount of overlap between neighbours. I predicted that if Riflemen were not territorial they would have more overlap of home ranges than Grey Warblers.

METHODS

Maps of home ranges were obtained using focal animal sampling techniques. Birds were located and followed for as long as was possible up to an hour and at one minute intervals during that period their position was plotted on a map of the study area. Accuracy was facilitated by a 30m x 30m grid marked throughout the study site and correspondingly represented on the map. The maximum error was about 7.5m. Two people were required for this task, one to watch the bird and one to determine the location and mark the map. Volunteers helped with data collection and several people worked in different parts of the bush simultaneously.

Plastic overhead projector sheets were placed over each map and polygons drawn around the outermost points. The area the polygons represented was calculated by placing a gridded sheet behind the clear sheet.and counting the squares within the polygon. Each grid square represented a known area.

Division of the data set into each of the four breeding stages resulted in sample sizes too small for stastical analysis, therefore comparison, for Riflemen, was restricted to three breeding stages 1.pre-breed/egglaying, 2.incubation/nestling and 3. fledge. Grey Warblers had a high nest failure rate due to drought and high winds, and few

pairs completed incubation. Consequently only pre-breed/egglaying data were available for this species. During the prebreed/egglaying and fledge periods pairs were usually together, and so data were for pairs rather than individuals for these two parts of the season. For the incubation/nestling period data were for individuals.

The difficulty of maintaining contact with a bird for a determinate period of time meant that the length of the sampling periods varied, also the number of sampling periods per individual varied. Home range areas (hr-areas) were only calculated where birds had been followed for a minimum of ninety minutes over at least two sampling periods, this meant that sample sizes were small, especially for Grey Warbler.

A hr-area was calculated for each map and the areas for each individual or pair, for each breeding stage, were added and then the overlapping areas subtracted.

Percent area overlap was estimated by drawing all the home ranges, for a particular period, onto one map that was on tracing paper, placing the grid squares behind it and counting all the squares in the overlapping areas.

The Mann-Whitney U test was used to test for differences between sexes and between species. The Kruskal-Wallis test was used to test for differences among the parts of the breeding period.

RESULTS

The population densities for Riflemen and Grey Warblers in the study area were similar, for Riflemen there were 15 pairs and 1 solo male, and for Grey Warbler there were 13 pairs and 4 solo males.

Area

The average size of Riflemen home ranges increased slightly across the three stages of the breeding season, however, the difference was not significant ($p > 0.05$) (Fig.1) .

During the incubation/nestling period, when male and female Riflemen foraged independantly, they occupied a similar sized area, and no significant difference was found between them ($p > 0.05$) (Fig. 2).

Grey Warblers had larger average hr-areas than Riflemen during the prebreed/egglay period (Fig.1), however, the sample size for Grey Warblers was too small to allow statistical comparison.

Overlap

With the exception of one pair, (the other pair, with which they overlaped, were not included in the analysis because they did not meet the minimum requirements of sampling time and number of samples), Riflemen had only a small ammount of home range overlap during the prebreed/egglay period. Overlap increased slightly, though not significantly, during the succeeding periods (Table.1, Fig.3). The overlap of 53% found for one pair was not typical of the other Riflemen, for which four had no overlap and two overlapped each other by only 2%. The overlap was found to be statistically significantly greater in the fledge period than in the pre-breed/egglay when the exceptional pair was omitted from the analysis ($p < 0.05$).

Grey Warblers had more overlap during the prebreed/egglay period than Riflemen (Table.1, Fig.3). However, the sample size for Grey Warbler was too small to allow statistical analysis. Only 3 pairs of Grey Warbler met the criteria for analysis, however, of the 5 which did not meet the criteria 3 exhibited overlap of 6%, 11% and 16%. It is likely that these figures represent a minimum estimate for these pairs because any increase in area found by more extensive sampling would have them encroaching on neighbours other than those which they are already overlapping. For

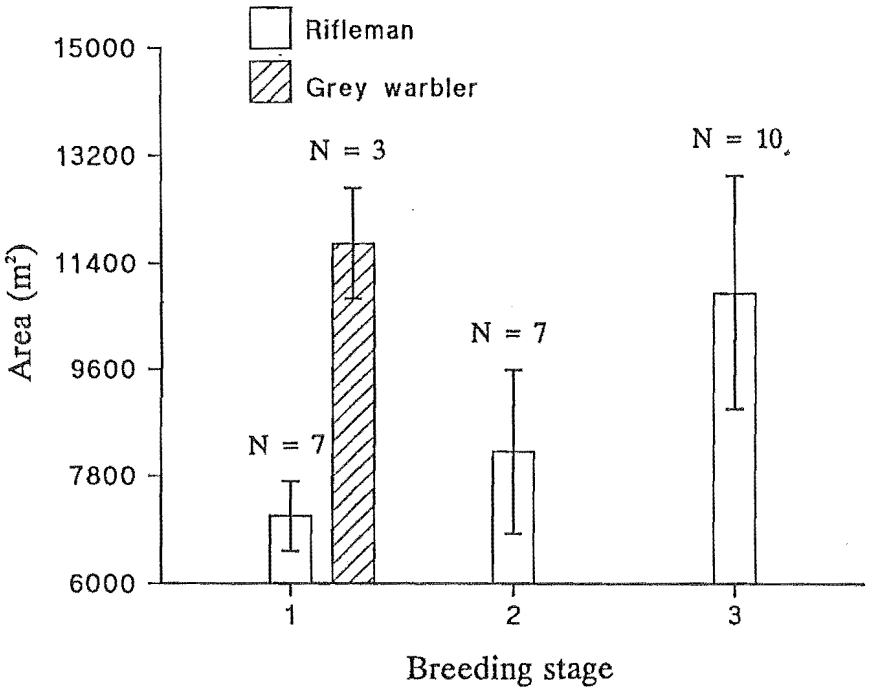


Figure 1. *The average home range area of riflemen and grey warbler during different stages of the breeding season. 1 = Pre breed/egg lay, 2 = Incubation/nesting, 3 = Fledge.*

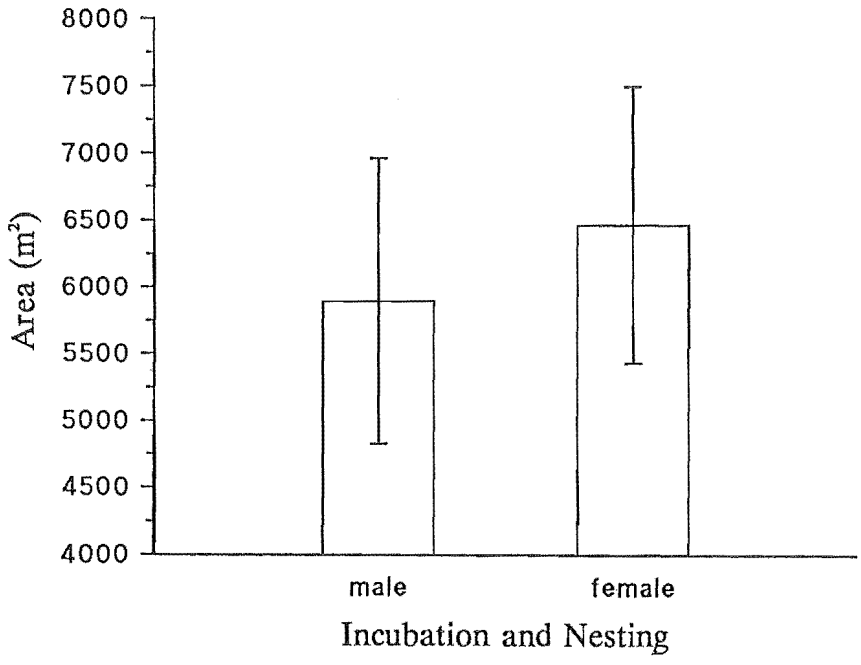


Figure 2. *The average home range area of female and male riflemen during the incubation/nesting period.*

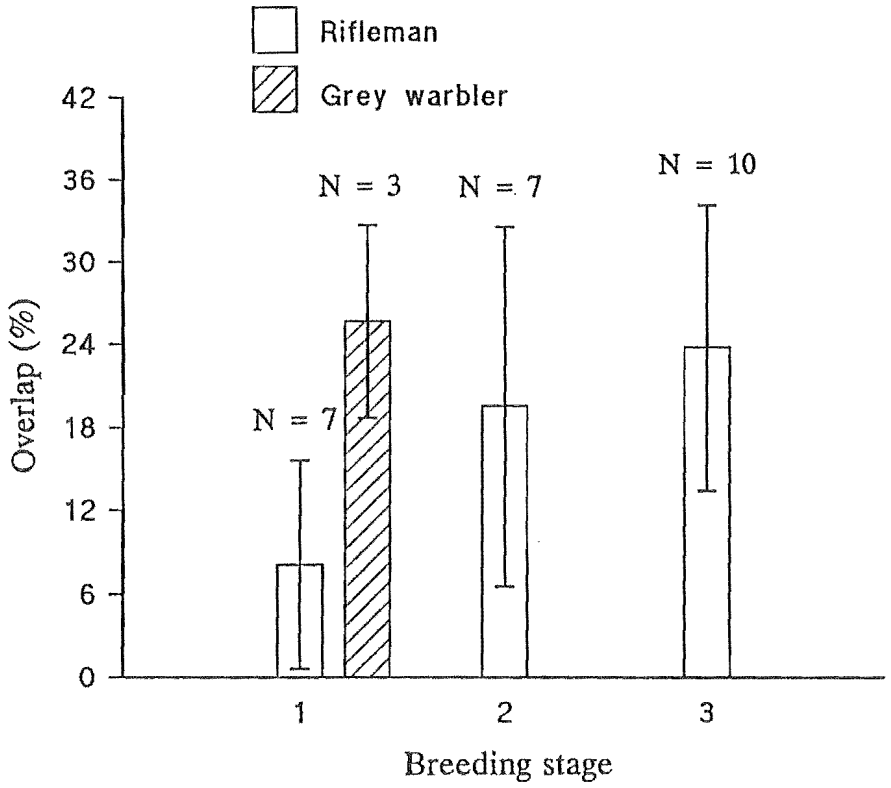


Figure 3. *The average home range overlap of riflemen and grey warbler during different stages of the breeding season. 1 = Pre breed/Egg lay, 2 = Incubation/nesting, 3 = Fledge.*

the two Grey Warbler pairs that did not overlap one pair was only sampled once for 42 minutes. Outside of sampling times they were observed to overlap to some extent.

Table.1 *The percentage of each pairs home range that was overlapped during different stages of the breeding season.*

	RIFLEMAN		GREY WARBLER	
	PB/EL	INC/NE	FLEDG	PB/EL
	53	71	89	30
	2	56	82	12
	2	0	0	35
	0	0	3	
	0	6	1	
	0	4	1	
	0	0	1	
			6	
			9	
			57	
			13	
MEAN	8.1	22.8	23.8	25.6
STD.D	19.8	31.90	34.6	12.1

PB/EL = Pre breed/Egglay, INC/NE = Incubation/Nestling, FLEDG =Fledge.

SUMMARY OF RESULTS

Bjorklund & Westman (1986) suggest that if mate guarding occurs, and is also beneficial to the female, the pair should minimise the probability of encountering other males during the fertile period by decreasing the utilised area of their home range. This could account for the slightly smaller home range of Rifleman during the prebreed/ egglay period. The decreased area during the early part of the season may also have been related to nest building activities; however during the second part of the breeding period the birds were also concentrated on the nest and the hr-area increased slightly, though not significantly. Any pattern of reduced home range use in the prebreed/egglay was more likely to be associated with mate guarding and avoidance of other males than nestbuilding activity. The use of the home range during the fledge period appeared to be determined by the chicks wandering, consequently the home ranges were larger during this period.

Brown & Orians (1970) suggested that there is a theoretically optimal foraging radius around the nest. If the theory is correct male and female Riflemen, who are both involved with incubation and brooding, should utilise a similar area. In this study female and male Rifleman did utilise a similar sized area during the incubation/nestling period.

Grey Warbler home ranges were larger than those of Rifleman, perhaps because Grey Warblers actively patrol and defend their territories and Rifleman do not. The Grey Warbler males will often interupt their foraging to fly to another part of their territory, or will go on patrol flights around the territory. Rifleman, on the other hand, rarely went on long flights, except when leaving the nest after incubation and to return to it after foraging. They moved slowly about the home range as they foraged and would not necessarily visit all of it in one day.

Despite the time and energy that male Grey Warblers expended on territorial defence the overlap of their home ranges was greater than that of Rifleman. The

greater overlap may point to one of the reasons why Grey Warblers need to actively defend their territories; their territories are constantly being encroached upon by other males. Most Riflemen pairs exhibited very little overlap, suggesting maintenance of exclusive areas. Exclusive areas were probably maintained by mutual avoidance. Riflemen, when they encountered neighbouring pairs while foraging, would often stay in proximity to each other for a few minutes but would eventually move off in different directions. Usually no interactions were observed on these occasions, at least none that the human observer could detect. The two pairs of Rifleman that overlapped each other significantly were closely related, the female of one pair was the daughter of the other, and the daughters partner was the son of a neighbouring pair. The daughter and her mate were tolerated in the parents home range, and vice versa, and the daughter and her mate helped to feed the parents chicks, (Rifleman are known to sometimes have helpers at the nest). However, the single chick of the younger pair was seen to be attacked on several occasions by the male of the older pair, the attacks were very aggressive with the attacker repeatedly diving and swooping at the chick and pecking at it. This intolerance of the strange chick may have been related to territorial behaviour. The chick was not recognised as a neighbour, or helper offspring so was attacked. The chick unfortunately was rather helpless and did not retaliate or move away and so was subjected to repeated attacks. The parents of the chick, although present on at least two of these occasions made no attempt to defend the chick, and indeed on one occasion the father of the chick flew away from the scene with food in its beak that it fed to the aggressors (father in laws) chicks.

Brown (1969) and Brown & Orians (1970) discuss the effect of population density on the reproductive success of individuals, and it is interesting to note that in the localised high density situation of the two significantly overlapping pairs, the younger pair only produced one offspring and two infertile eggs, while the older pair produced 4. The same two pairs bred in the same nest boxes the previous year with

the same outcome, the younger pair produced only 1 chick out of 4 eggs and the older pair 3 chicks. Though this is an isolated case, and there may be other explanations, it could point to the disadvantages of not maintaining an exclusive feeding resource during the breeding season, and explain why the other Rifleman pairs in this population had exclusive home ranges.

Both Rifleman and Grey Warbler have a regular pattern of dispersion over the study area, and this tends to be characteristic of territorial individuals (Brown 1969)

The exclusive areas, maintained through mutual avoidance, found in Riflemen, by the definition of some authors constitute territories (Scoener 1968, Pitelka 1959 citrd in Brown & Orians 1970 & Schoener 1968, Davies & Houston 1984).

MATE GUARDING

INTRODUCTION

Males can never be as assured of their paternity of the offspring that they help to raise, as females are of their maternity, and if males work to raise unrelated offspring they will suffer a large cost in lost reproductive success (Trivers 1985). Conversely, the potentially large reproductive benefits resulting from any increase in paternity should make it advantageous for males to copulate whenever they get the chance. Extra pair copulation is known to occur in at least 104 bird species (Edinger 1988), and several studies have shown multiple paternity within clutches (Mumme et al. 1985, Gavin & Bollinger 1985, Westneat 1987). Edinger (1988) found that male Orioles *(Icterus galbula)* were more likely to intrude on another male's territory during the females fertilisable period; Birkhead (1979) also found this with Magpies *(Pica pica)*

If cuckoldry is frequent, behavioural strategies are likely to evolve that would reduce a males probability of being cuckolded (Lifjeld & Slagsvold 1989, Birkhead 1987). Birkhead (1987) suggested two strategies for males to avoid being cuckolded; mate guarding and frequent copulation (but see Lumpkin 1981). Frequent copulation was suggested as a device for concealing the fertile period of the female, by copulating before and after the fertile period as well as during it other males would not be able to use copulation as a signal of female fertility. Frequent copulation would also ensure a copious amount of the males own sperm in the females reproductive tract. Evidence from chickens shows that the probability of paternity is proportional to the number of spermatozoa from each male (Birkhead 1987). Mate guarding behaviour has been reported in over 50 bird species, mainly passerines (Birkhead 1987).

I investigated the courtship spacing relationships of Riflemen and Grey Warblers

to determine whether or not mate guarding occurs in these species.

METHODS

Mate guarding data were gathered using focal animal sampling methods. During a 10 min. sampling period instantaneous samples of behaviour were recorded every minute. Observations were of breeding pairs foraging together during the prebreed and egglaying periods of the breeding season. The distance between the male and female, and their spatial relationship were recorded. The distance was recorded as one of the distance classes 0-1, 1-2, 3-4, 4-5 and 5+. The spatial relationship was recorded as the males position with respect to the female: he was either above her, below her or horizontal to her. If either bird was lost to sight or it was uncertain which bird was which the relationship was recorded as unknown.

Percentage frequency values for each distance class were calculated for each pair and a Mann Whitney U test was used to compare each distance class between the species. The average frequency values for each distance class were plotted showing standard errors.

The mean occurence of each spatial category was calculated for each pair, and a Kruskall Wallis test was used for comparison among the categories for each species. The mean of the means were plotted showing standard errors.

Pairs with less than six observations were not used in the analysis.

Observations were made in both 1988 and 1989 and the data for each year were analysed separately.

RESULTS

Distance

Grey Warbler males spent most of their time close to the females, whereas Riflemen spent most of their time at a distance from the female (Fig. 1.).

Grey Warbler males spent significantly more time within a meter of the female than the male Riflemen did, and Riflemen spent significantly more time at least four meters or more away from the female than the Grey Warbler in 1988. In 1989 Grey Warbler males spent significantly more time within one meter of the female than male Riflemen did, and male Riflemen spent significantly more time between two and four and greater than five meters away from the female than the Grey Warbler males did (Table 1).

Table 1. *Results of Mann Whitney U tests comparing the distance between male and female during the pre-breed/egglaying period. The frequency of each distance class was compared.*

	DISTANCE CLASS (m)					
	0-1	1-2	2-3	3-4	4-5	5+
1988	*	ns	ns	ns	*	***
1989	**	ns	*	*	ns	**

ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Spatial Relationship

The males of both species spent most of their time below the female. The overall patterns were also similar with the greatest amount of time being spent below the female and the least amount above (fig.s 2 & 3). The significance of the patterns of spatial relationship were different in each species; in the Riflemen there was no

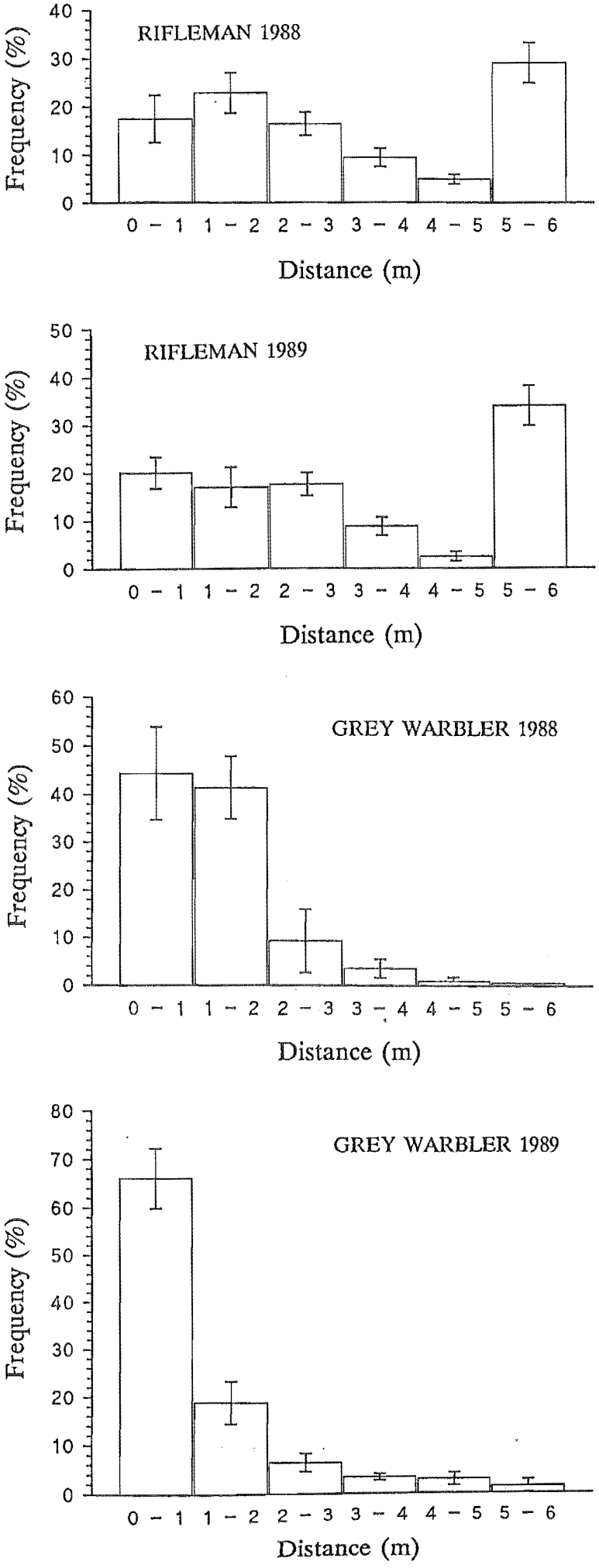


Figure 1. *The distance between the male and female during the pre breed and egg laying period.*

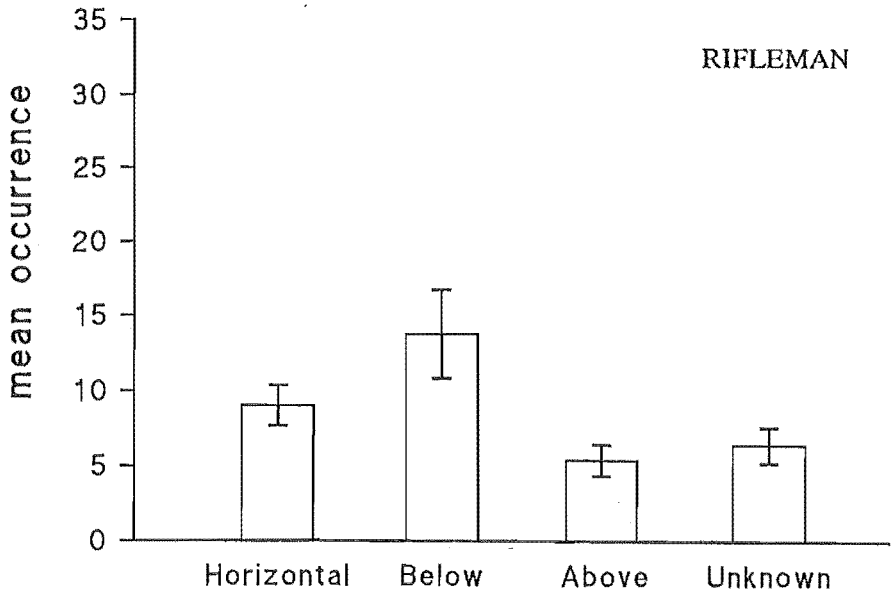


Figure 2. *The spatial relationship of the male to the female during the pre breed/egg laying period.*

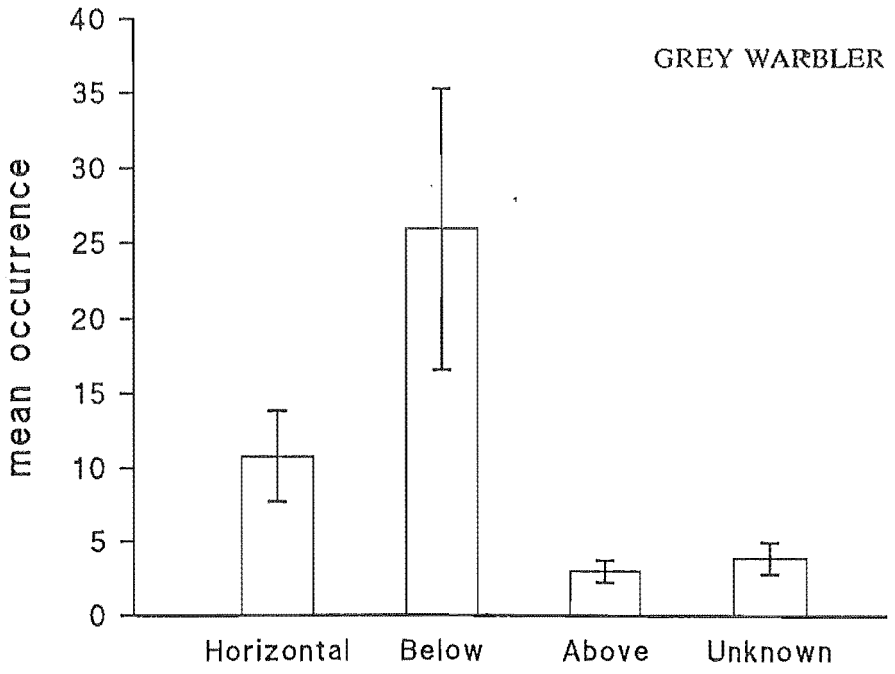


Figure 3. *The spatial relationship of the male to the female during the pre breed/egg laying period.*

statistical difference among the categories ($p > 0.05$), whereas in the Grey Warbler the differences among the categories were statistically significant ($p < 0.01$).

SUMMARY OF RESULTS

The results of this study suggest that male Grey Warblers guard their mates during the pre-breed egglaying period.

Male Rifleman were often quite a long distance from the female and this suggests that if Rifleman in any way try to avoid cuckoldry mate guarding is probably not the mechanism. However, the pattern of spatial relationship to the female, in which the male tends to be lower than the female, suggests that he might be keeping an eye on her. It would be easier to see her from a position lower than she. Mutual avoidance, as indicated by the smaller home ranges during the pre-breed period, is more likely to be the mechanism for avoiding cuckoldry. Copulation is infrequent among Rifleman and was rarely seen, so evidence of extra pair copulation was also not found. Studies to determine parentage within clutches would give a usefull insight as to whether extra pair copulation is occurring.

OVERALL DISCUSSION

Female Riflemen are slightly larger than female Grey Warblers and lay a slightly larger clutch, Riflemen have more secure nests than Grey Warbler, have a higher annual rate of mortality and, at Kowhai Bush, appear to have a slightly more diverse diet. These subtle differences in the ecology, morphology and life histories of Riflemen and Grey Warblers may account for some of the differences in their time budget, spacing and guarding behaviour.

Birds with more secure nests, such as hole nesters, tend to have larger average clutch sizes than those with open nests (Lack 1968). The clutch of the hole nesting Riflemen is on average about 12% larger than that of the arboreal Grey Warblers. This difference in clutch size may be determined by differences in predation pressure; large clutches may attract more attention from predators through increased noise and more frequent visits by parents. If the nest location is readily accessible to predators then smaller clutch sizes may prove more successful (Woinarski 1989). Reserving energy for replacement clutches may also be important. Grey Warblers, at Kowhai Bush, had a high nest failure rate, de Hamel (1989) calculated a 79% nest failure rate for the 1987/88 year. The main causes of nest failure in Grey Warbler were predation, brood parasitism by the Shining Cuckoo *(Chrysoccyx lucidus)*, nest desertion and blow out in high winds (Gill 1980, pers.obs.). Woinarski (1989) also found a high rate of nest failure amongst three species of *Gerygone* in south-eastern Australia. The main cause of failure amongst the Australian species was predation, but desertion and falling to ground were also significant factors. The Australian species, like Grey Warbler, are foliage gleaners and nest in the foliage (Woinarski 1989). Evidence of high nest failure in other members of the genus suggests a long history of high nest failure rate in Grey Warbler, and it may therefore have had some influence on other life history characteristics. Rifleman, at the Kowhai Bush study site, used nest boxes

and their nest failure during the 1988/89 and 1989/90 seasons were 14% and 13% respectively. Of the four failures during the two seasons, three were due to abandonment, of which at least two were caused by human disturbance, and the fourth was due to infertility. The use of nest boxes for breeding undoubtedly reduced nest failure rate in Rifleman, however, natural breeding sites, such as holes in tree trunks well above the ground, holes in fence posts, holes in the ground, among dead branches on the ground, under the eaves of sheds and in holes in banks (Gray & Gaze 1985, Gray 197 , pers. obs.), probably still afford a good success rate. The success rate afforded to Rifleman by hole nests would have been greater before the introduction of mammalian predators, when the main predators would have been avian (Holdaway 1989). Rifleman have white eggs, which is characteristic of hole nesting species of longer standing (Woinarski 1989), suggesting that hole nesting is not a recent adaptation and may therefore have had some influence on other life history characteristics, such as clutch size.

Larger clutches require more energy to produce and result in more chicks which again require more energy to feed. The greater energy requirements of larger clutches and broods may have necessitated the increased parental investment of the male Rifleman.

Grey Warbler have an annual mortality rate of 18.5% which is much lower than the estimated 40% of Rifleman. A lower mortality rate gives Grey Warbler potential for greater long term reproductive output and may reduce the significance of low annual reproductive success. A higher mortality rate in Riflemen means that chick survival from year to year is important because for any given individual there may not be many reproductive opportunities. This may have influenced the type of nest that Riflemen build, the more secure nest ensuring greater chick survival, and greater chick survival favouring larger clutches.

The large proportions of time allocated to alert perching in Grey Warbler may be attributable to predation risk, and brood parasitism. High risk of predation and parasitism would favour, a time and energy commitment to predator and parasite avoidance. Territory defence may also reduce the risk of predation by spacing the nests to make them less obvious (Hinde 1956).

Larger clutch sizes in Riflemen notwithstanding, the female Grey Warbler is slightly smaller than the female Rifleman and her clutch size to body weight ratio is higher than that of female Riflemen. Yet the female Grey Warbler does not have the help with parental care from the male that the female Rifleman has. There may be differences in foraging efficiency that could account for this. The diet of the two species differs, with the Grey Warblers at Kowhai Bush appearing to be more specialised (see general introduction). However, the study site at Kowhai Bush is highly modified and lacking in the heterogeneity and vertical structure of less modified habitat, and the diet may not be typical of Grey Warblers in other habitats. (Although Grey Warblers occupy a wide range of habitats and probably do not have a typical diet). Riflemen forage mostly on the trunks of trees and Grey Warblers forage mostly in the canopy (McLean & Dean Unpub). The canopy is more continuous and therefore enables gradual progression, whereas feeding on trunks requires flight from one to the next. Because of their different foraging locations, Riflemen tend to fly more than female Grey Warblers, interrupting foraging and probably using more energy. Sullivan (1990) found that differences in foraging efficiency between recently independent and more experienced juvenile juncos *(Junco phaeonotus)* had significant effects on daily time allocations, body mass and mortality. Wolf et al.(1975) found that sunbirds (Nectariniidae) require a higher foraging efficiency (total energy intake divide by total energy spent foraging) than humming birds (Trochilidae) because of their lower foraging costs per unit time, but that this was balanced by the lower extraction efficiency of hummingbirds. These examples show that variation in foraging efficiency

can have significant effects on energy budgets. However, (Ettinger & King cited in Finch 1984) suggested that the "do nothing" component of the time budget has a stabilising effect on energy budgets and could dampen variation in foraging efficiency reducing its effect on time budgets.

Food is a limiting factor for small insectivorous birds such as the Rifleman (Morse 1971), and they must spend a large proportion of their time feeding to maintain the necessary energy levels for survival and reproduction. The constraints imposed by food limitation, their small size (Sherley 1985), the high energy requirements and consequences of large clutch size and the males substantial contribution to parental care place further constraints on the time and energy available to Riflemen for other activity demands. Maintenance of territory by means of aggression, advertisement and patrolling is quite expensive, in terms of maximising genetic fitness and the disadvantages or costs probably outweigh the advantages.

Another explanation for the lack of aggressive defense of territories in Riflemen may be in the nature of territorial disputes or contests. Contests are usually settled by asymmetries between the contestants that reflect physical advantages, and energy reserves may often be an important asymmetry in animal contests (Marden & Waage 1990). Because of the time and energy constraints imposed on Rifleman there may be no reserves to allow asymmetries to occur, no individual would have any advantage over another therefore mutual avoidance is more likely to occur than aggression. That mutual avoidance occurs is supported by the observations that neighbouring Rifleman brought into proximity by chance meandering might get quite close to each other and even mingle for brief periods, but will always move away in different directions quite soon after. Theoretically, an individual that was genetically disposed to having more energy reserves than other individuals might have an advantage in territorial disputes and therefore become more aggressively territorial. However, this may not be possible in Riflemen. The only advantages of aggression over mutual avoidance, as a

mechanism for maintaining exclusive areas, would be that larger territories could be maintained. Larger territories may not be an advantage to the Rifleman in Kowhai Bush, however, other populations with a higher density may show higher levels of aggression.

The levels of alertness associated with aggressive maintenance of a territory may have advantages in detecting predators, however, nest predation is low in Rifleman so this is probably not so important for them.

Although Grey Warbler are similar in size to Riflemen, in fact they are smaller than the female Rifleman, the influences under which they operate are slightly different and result in a slightly different cost-benefit trade-off. Grey Warbler are subject to higher levels of predation than Rifleman, and this ramifies into smaller clutch sizes, reduced parental care and aggressive territorial defence.

ACKNOWLEDGMENTS

I would like to thank the many people who, in many different ways have contributed to the achievement of this thesis.

Firstly my family, who have always been a source of strength and who have believed in me and supported me in all that I have done, especially Alison and Brian and Fraser and Samuel who took me into their home.

My supervisor Ian McLean, especially for showing me the birds, but also for the considerable time he spent teaching me in the field, and the various and numerous unimaginable other things that inevitably come up during the course of a project like this.

Saskia and Peter Wood who took me into their home and on many occasions provided warmth, sustenance and a welcome after long days in the field.

The volunteers from the Earthwatch organisation, who came "All The Way From America", except Valerie of course who came from Australia, to help with the field work: Laurie Allan, Riley Wheeler, Audrey Gilmour, Bill Lillibridge, Valerie Steele, Connie Douglas, Gloria Zager, Jane Kruze, Pat Taber, Jack Ross, Kurt Kiffman, Don Sorby, Jacquie Sorby, Sherri Fresonke, Marjo Norton, Elaine Vak, Jayce Anderson.

Sue Mackle, on whose property the birds live, and who kindly allowed us access to them.

Jack, Hine and Dean at the field station in Kaikoura who helped to make living there that much easier.

Fiona Proffitt for her help in the field.

Mike Winterbourn and Richard Holdaway for making some very complicated sentences more reader friendly.

All the people who helped, in those final hectic days before the deadline, with the final production stages: Tracey Robinson, Jan McKenzie, Lindsay Chadderton,

Richard Harris, Richard Maloney, William Titulaer and Andrew Van Olphen (for chocolate).

The class of '88, I'm glad we got to know each other.

The staff and students of the Zoology Department.

And finally all my friends who have remained supportive despite much neglect.

Banding was done under a Dept. of Conservation banding permit issued to the Department of Zoology, University of Canterbury.

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APPENDIX 1

Means and standard errors of average percentage time allocation for rifleman and grey warblers.

Whole nesting period.

	Behaviours						
	1	2	3	4	5	6	7
Female rifleman							
Means	88.3	0.8	2.5	4.1	2.4	1.1	0.8
± 1SE	2.5	0.4	1.2	1.3	0.7	0.5	0.4
Male rifleman							
Means	83.9	4.9	2.7	2.8	1.8	2.7	1.1
± 1SE	3.3	2.7	1.2	0.9	0.6	1.2	0.2
Female grey warbler							
Means	81.5	2.4	0.3	3.7	8.3	3.3	0.8
± 1SE	4.3	1.3	0.3	1.8	4.4	1.7	0.8
Male grey warbler							
Means	42.4	-	4.9	8.9	5.0	37.2	1.7
± 1SE	3.5	-	2.0	2.5	1.8	5.3	1.0

APPENDIX 2

Means and standard errors of average percentage time allocation for rifleman during the early and late nesting periods.

	Rifleman						
	Behaviours						
	1	2	3	4	5	6	7
Early Nesting period Male							
Means	79.8	9.4	2.2	5.1	0.8	2.6	-
± 1SE	5.6	5.2	1.1	1.5	0.4	1.9	-
Female							
Means	86.3	1.5	2.3	5.1	2.7	2.2	-
± 1SE	3.4	1.1	1.4	2.2	1.1	1.1	-
Late nesting period Male							
Means	85.5	2.7	2.2	0.8	3.1	2.9	2.7
± 1SE	3.2	1.8	0.6	0.5	1.2	1.1	1.1
Female							
Means	87.9	0.5	2.3	3.1	3.42	0.6	2.1
± 1SE	2.6	0.3	0.8	1.1	1.1	0.4	0.9

APPENDIX 3

Means and standard errors of average percentage time allocation for grey warblers during the early and late nesting periods.

	Grey warbler						
	Behaviours						
	1	2	3	4	5	6	7
Early nesting period							
Male							
Means	53.7	0	2.7	6.4	3.4	33.8	-
± SE	7.2	0	1.0	4.6	1.2	7.5	-
Female							
Means	83.5	1.9	0.4	5.4	5.9	2.9	-
± SE	4.7	1.3	0.4	2.2	3.0	1.9	-
Late nesting period							
Male							
Means	36.3	0	4.6	13.2	7.9	35.5	2.5
± 1SE	4.7	0	2.7	4.4	4.8	5.0	1.3
Female							
Means	77.6	0	0	0	9.62	10.7	2.1
± 1SE	9.3	0	0	0	8.3	9.3	1.8